

BONE LOSS FROM CARCASSES IN MEDITERRANEAN ECOSYSTEMS

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ABSTRACT: In order to interpret fossil and sub-fossil associations of vertebrates, it is important to understand how carcasses degrade in nature. Here we describe the process of bone loss from 32 carcasses from eight species of terrestrial mammals over two to 63 months in two Mediterranean ecosystems in the southwest of the Iberian Peninsula. The carcasses ranged in mass from 5 kg to over 450 kg. These data allow the quantitative description of the dynamics of degradation in three time phases defined by changes in the rate of bone loss as measured by the Skeletal Conservation Index (SCI). The SCI values estimated for each phase of degradation is considered the fossil potentiality of the carcass. In the first phase, very few bones were lost, followed by a phase of high bone loss driven by scavengers. The rate of bone loss reduced greatly again in the final phase, which was driven primarily by abiotic, environmental factors. The largest carcasses spend a longer time in each phase, and also had a higher SCI at the end of Phase II. The smallest carcasses experienced a much higher variance in degradation, had significantly lower SCI, and many of the smallest carcasses were consumed completely in a short period of time. Differences between localities were observed regarding SCI values. Presence or absence of tree coverage in the place where the carcass was located also had a significant effect on SCI. These data highlight the importance of considering the contemporaneous scavengers when interpreting animals from paleontological contexts. These data also explain the bias observed in many ancient sites whereby larger animals are over represented.

INTRODUCTION

After death, many factors act to degrade carcasses in natural ecosystems. Environmental abiotic (Behrensmeyer 1978) and biotic factors contribute to the process. Abiotic factors could include the weather (i.e., temperature, precipitation); and biotic factors could include microorganisms, insects and their larvae, and scavengers (Behrensmeyer et al. 1979; Denys 2002; Hedges 2002; Cáceres et al. 2009; Moleón et al. 2015). Although many species scavenge in terrestrial ecosystems, few animals can process bones from carcasses weighing over 50 kg, a size class that encompasses the majority of known vertebrate taphocoenosis analyzed (Bernáldez Sánchez 2011; Western and Behrensmeyer 2009). Scavenging is important for the proper functioning of an ecosystem, and may be an easy meal, but it does require adaptations in the immunological and digestive systems in order to avoid septicaemia, thus limiting the species that can partake. Scavenging also presents logistical obstacles to smaller animals that may not be able to break the hide or bone of a large animal, and thus may depend on larger scavengers or the elements to open the carcass. This may suggest that the scavenging community as a whole may be important in the degradation of carcasses (Faith and Behrensmeyer 2006).

Understanding the post-mortem dynamics of carcasses in nature is fundamental for understanding the fossil record (Weigelt 1927; Behrensmeyer et al. 1979; Behrensmeyer and Miller 2012; Lyman 2010), and few experiments have measured these effects (Andrews and Evans 1983; Bernáldez Sánchez 2009; D'Andrea and Gotthardt 1984; Domínguez-Rodrigo 2001; Lansing et al. 2009; Mondini and Muñoz 2008; Reed 2009; Sutcliffe 1970; White and Diedrich 2012; Yravedra Sainz de los Terreros et al. 2012). Behrensmeyer and Boaz (1980) described the effects of scavenging on an assemblage of ungulates in Amboseli National Park

(Kenya), and they found selective consumption of carcasses, especially by hyenas. Carcasses over 50 kg experienced better conservation than carcasses with less corporal mass, implying a disproportionately higher representation of the heaviest species at subsequent taphocoenosis. They called this probability the “fossil potential” of the species.

Here we quantify the process of degradation of carcasses in the Mediterranean ecosystem of southwest Iberia through time for three size classes of carcasses monitored over two to 63 months using the Skeletal Conservation Index (SCI). Using these data we calculate the fossil potential of different size classes, and test for statistically significant differences in preservation across time between size classes resulting in a model that explains the most important factors that determine the pattern and speed of bone loss from a carcass in the context of paleontology.

STUDY AREA

This experiment took place in two Mediterranean ecosystem parks that are less than 200 km away from each other (Fig. 1). One is the Doñana Biological Reserve (Huelva, Spain; RBD). The other is the Sierra Norte de Sevilla Natural Park (Seville, Spain; SNS), which is part of the Sierra Morena mountain range. The carcasses were monitored in RBD from 1988 to 1991 and in SNS from 2004 to 2010.

RBD has an area of 7,600 ha and contains a dune area with very little vegetation, a seasonally flooding marsh area, a shrubby Mediterranean habitat, and a long ecotone between the marsh and Mediterranean habitat locally referred to as the “Vera”. Oak is present at low density (isolated trees) in the Mediterranean and ecotone habitats, and there are pine groves in the Mediterranean habitat. Both live and dead animals are found at a higher density in the ecotone habitat (Bernáldez Sánchez 2011). The park

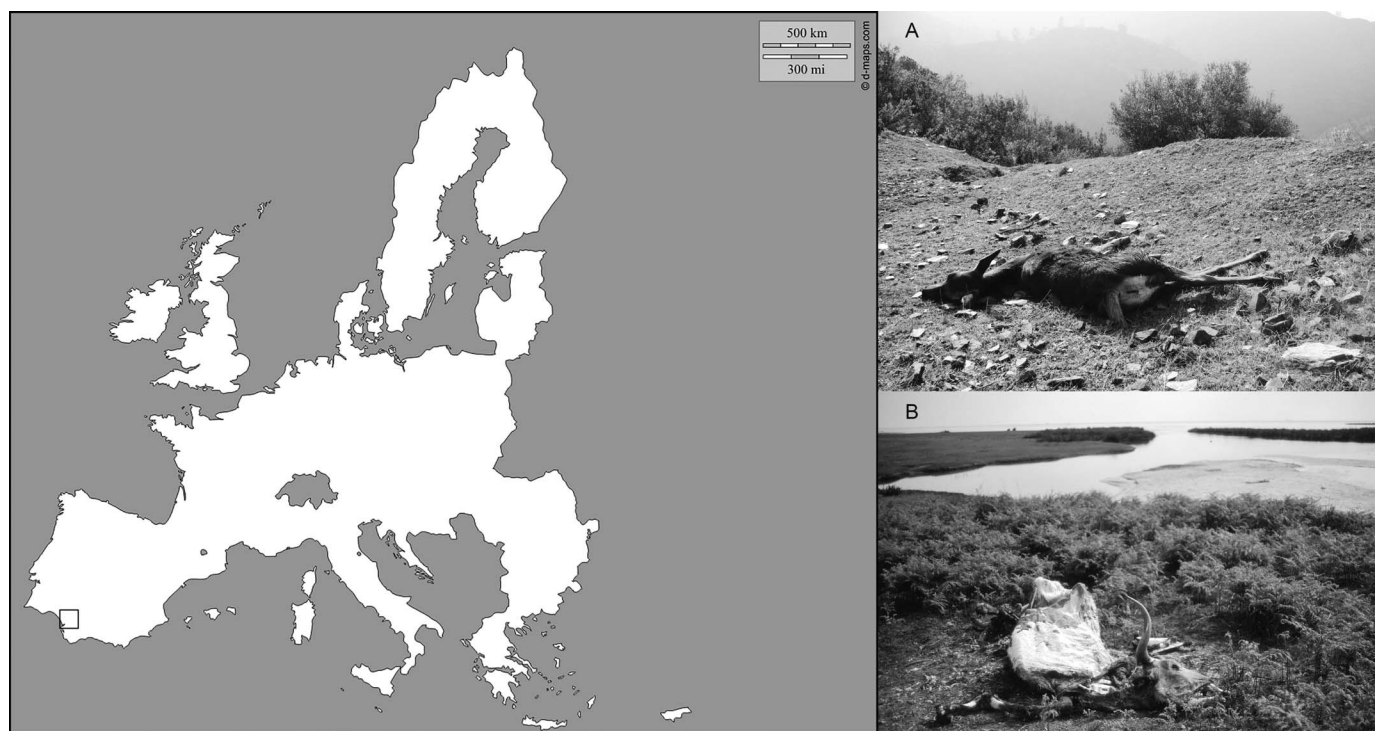


FIG. 1.—Photos of the two Mediterranean habitats in southwest Iberia where observations took place, and their general location on the Iberian Peninsula. **A**) Sierra Norte Nature Park in the province of Seville (SNS). **B**) Doñana Biological Reserve in the province of Huelva (RBD).

extends from sea level to 40 m asl and has an average annual rainfall of 575 mm. The average annual temperature in RBD range between 16 and 19° C. Average maximum temperature in the summer is 35–40° C, and the average minimum in the winter is about 0° C. RBD has a high level of conservation protection including limited access. All carcasses studied in RBD came from animals that died natural deaths.

SNS has an area of 177,484 ha and a more homogenous oak woodland habitat. This experiment utilized the two parcels “Las Navas-El Berrocal” near the town Almadén de la Plata and “Upa” near the town Cazalla de la Sierra. The park extends from 260 to 968 m asl and has an average annual precipitation of 810 mm. The average annual temperature in SNS is 14–18° C. The average maximum in the summer is 25–30°C, and the average minimum in the winter is 5–8° C. There is a hunting season in this park, and the red deer carcasses followed in this study from SNS were all hunted (for reasons other than this study).

METHODS

Observations of 32 carcasses located in RBD and SNS were included in this study. These carcasses were from eight different species ranging in size from 5 kg to over 450 kg (Table 1). The majority were from adults ($n = 25$), the rest were juveniles ($n = 7$). Carcasses from six species of mammals were monitored in RBD: three horses (*Equus caballus*, one adult and two 2-years-old juveniles), three cattle (*Bos taurus*, two adults and one yearling), five adult red deer (*Cervus elaphus*), four fallow deer (*Dama dama*, three adults and one juvenile), three adult wild boars (*Sus scrofa*), and one adult fox (*Vulpes vulpes*). Carcasses from three species of mammals were incorporated into the study from SNS: one adult mongoose (*Herpestes ichneumon*), one adult badger (*Meles meles*), and 11 red deer (eight adults and three juveniles).

In most cases carcasses were monitored from the day the animal died ($n = 24$). In the remaining cases ($n = 8$), the date of death was established by rangers' reports. Monitoring was done regularly. Observations were taken

approximately weekly in the first stage when soft tissue was still present, and then the frequency of observations was reduced to every month or two. Carcasses were monitored for an average of 21 months, range 2.4 months to five years and three months (Table 1). Observations consisted of visual inspection and photographic record. Several characteristics of the carcasses were recorded: species, state of carcass at first observation (starting condition: complete body or without soft tissue), age of the individual when death occurred (adult or juvenile), degree of tree coverage in the place where the carcass was lying (presence or absence), and approximate mass of the carcass. The carcasses were classified in three size classes depending on the approximated body mass at time of death, according to Bernáldez Sánchez (2009, 2011): Class I, carcasses over 200 kg; Class II, carcasses 50 to 200 kg; and Class III, carcasses from about five to 50 kg. The number of bones remaining in the carcass was also recorded at each observation, and used to calculate an SCI (eq. 1) for each carcass and observation. The SCI was used to quantify the preservation of the carcass at each observation. This index quantifies the proportion of conserved bones in reference to the total number of bones in each species.

$$SCI = (NB/NS \times MNI) \quad (1)$$

Where NB is the number of bones observed in the carcass at each observation, and NS is the number of bones that make up the skeleton of an individual. In cases where the number of individuals is not one or is not known, such as in most paleontological sites, the minimum number of individuals (MNI) should be taken into account. MNI was equal to one for all the carcasses studied here.

Analysis of Degradation Dynamics

The dynamics of bone loss was studied by modeling SCI values in each observation with Generalized Linear Mixed Models (GLMMs) as a function of time and class as explanatory variables of interest. Variable

TABLE 1.—Table of the 32 carcasses monitored in Mediterranean ecosystems. Data for each individual include: reference of the carcass (ID), species, locality (RBD = Doñana Biological Reserve; SNS = Sierra Norte de Sevilla Natural Park), state of conservation of the carcass at the first observation (Start: C = complete; S = without soft tissue), age (A = adult; J = juvenile), approximate body mass (Mass, in kg), size class (Class: Class I = > 200 kg; Class II = 50 to 200 kg; Class III = about 5 to 50 kg), tree coverage around the carcass (Tree: 0 = absent; 1 = present), number of months over which carcass was observed (Time), and estimated Skeletal Conservation Index (SCI) at last survey. The three monitored carcasses excluded from analyses are in *italics* (see Discussion).

ID	Species	Locality	Start	Age	Mass (kg)	Class	Tree	Time (months)	SCI
Caballo2 ^{1,2}	<i>Equus caballus</i>	RBD	C	A	350	I	0	24	49.8
Vaca1 ^{1,2}	<i>Bos taurus</i>	RBD	C	A	450	I	0	17	45.3
Vaca2 ^{1,2}	<i>Bos taurus</i>	RBD	C	A	450	I	0	25	42.8
Vaca7	<i>Bos taurus</i>	RBD	C	J	250	I	0	13	48.8
Caballo1 ^{1,2}	<i>Equus caballus</i>	RBD	C	J	200	II	0	16	24.1
Caballo3 ^{1,2}	<i>Equus caballus</i>	RBD	C	J	175	II	0	2	22.1
Ciervo1	<i>Cervus elaphus</i>	RBD	C	A	100	II	1	2	98.0
Ciervo2	<i>Cervus elaphus</i>	RBD	C	A	100	II	1	63	7.3
Ciervo3	<i>Cervus elaphus</i>	RBD	C	A	100	II	1	63	5.4
Ciervo4	<i>Cervus elaphus</i>	RBD	C	A	100	II	0	27	4.5
Ciervo5 ¹	<i>Cervus elaphus</i>	RBD	C	A	100	II	1	5	38.1
Gamo2 ¹	<i>Dama dama</i>	RBD	C	A	65	II	0	14	31.7
Gamo4 ¹	<i>Dama dama</i>	RBD	C	A	65	II	1	5	60.0
Gamo5	<i>Dama dama</i>	RBD	C	A	65	II	1	17	15.6
Jabali1	<i>Sus scrofa</i>	RBD	C	A	54	II	1	17	10.8
Jabali2 ¹	<i>Sus scrofa</i>	RBD	C	A	50	II	0	5	20.8
Jabali3	<i>Sus scrofa</i>	RBD	C	A	54	II	0	24	10.8
1UPA ^{1,2}	<i>Cervus elaphus</i>	SNS	C	J	100	II	0	24	10.2
2UPA ^{1,2}	<i>Cervus elaphus</i>	SNS	C	A	100	II	1	11	0.0
3UPA ¹	<i>Cervus elaphus</i>	SNS	C	J	100	II	0	4	43.9
4UPA ^{1,2}	<i>Cervus elaphus</i>	SNS	C	J	100	II	1	24	5.9
6UPA ¹	<i>Cervus elaphus</i>	SNS	C	A	100	II	0	27	3.4
7UPA ^{1,2}	<i>Cervus elaphus</i>	SNS	C	A	100	II	1	27	3.4
11UPA ¹	<i>Cervus elaphus</i>	SNS	C	A	100	II	0	10	38.5
2NAVAS ^{1,2}	<i>Cervus elaphus</i>	SNS	S	A	100	II	0	50	0.0
5NAVAS	<i>Cervus elaphus</i>	SNS	S	A	100	II	0	27	0.0
10NAVAS	<i>Cervus elaphus</i>	SNS	S	A	100	II	0	10	19.0
8UPA	<i>Cervus elaphus</i>	SNS	C	A	100	II	0	14	0.0
Gamo3 ^{1,2}	<i>Dama dama</i>	RBD	C	J	5	III	0	18	0.0
Zorro ^{1,2}	<i>Vulpes vulpes</i>	RBD	C	A	5	III	1	11	6.0
9NAVAS	<i>Herpestes ichneumon</i>	SNS	C	A	5	III	1	46	99.9
12NAVAS	<i>Meles meles</i>	SNS	C	A	5	III	1	24	99.9

¹ Carcasses used to study SCI at the first inflection point in the degradation curve, between Phases I and II.

² Carcasses used to study SCI at the second inflection point in the degradation curve, between Phases II and III.

time was transformed to the negative exponential of time ($e^{-\text{time}}$) for a better adjustment of models to the data. Other fixed variables that could have had an effect on the degradation of the carcasses were added to the models so they could be controlled for. These variables were locality, species, starting condition, age, and tree coverage. To control for the effect of having repeated measurements per individual, individual identity was taken into account as a random variable. All variables were included in the initial model and then those that did not significantly affect SCI were excluded in later models. The final model only includes variables with a significant effect over SCI. Generalized Linear Mixed Models were run in R version 3.1.3 (R Core Team 2015) and constructed assuming a beta distribution by using the function `glmmadmb()` from the package `glmmADMB` version 0.8.0 (Fournier et al. 2012; Skaug et al. 2014). Model assumptions were assessed by visual examination of quantiles and residuals.

Phases of Degradation

To study changes in the velocity of carcass degradation in different moments of the disintegration process, we calculated the velocity of bone loss (p ; Bernáldez Sánchez 2011) between two observations as the

observed change of SCI between two consecutive observations divided by the time passed between them (eq. 2).

$$p = \left(\text{SCI}_{(n)} - \text{SCI}_{(n+1)} \right) / \left(T_{(n+1)} - T_{(n)} \right) * 100 \quad (2)$$

Where $\text{SCI}_{(n)}$ is the SCI for the “n” observation of the carcass, $\text{SCI}_{(n+1)}$ is the SCI for the consecutive observation of the carcass (observation “n+1”), and $T_{(n+1)} - T_{(n)}$ is the period of time between the two observations.

By calculating p between two observations, we identified different inflection points in the dynamics of degradation for each carcass when p changed markedly. We defined three phases in the degradation process according to these inflection points (see results). To study whether different classes of carcasses showed different SCI values when they changed from one phase to another occurred, we tested for differences in the SCI at the inflection points among size classes by using Generalized Linear Models (GLMs). Locality and tree coverage were added to the models to control for their effects. The same criteria as above were used for model selection. Generalized Linear Models were run in R version 3.1.3 (R Core Team 2015) and constructed assuming a beta distribution by using the function `betareg()` from the package `betareg` version 3.0-5 (Cribari-Neto and Zeileis 2010). Model assumptions were assessed as before.

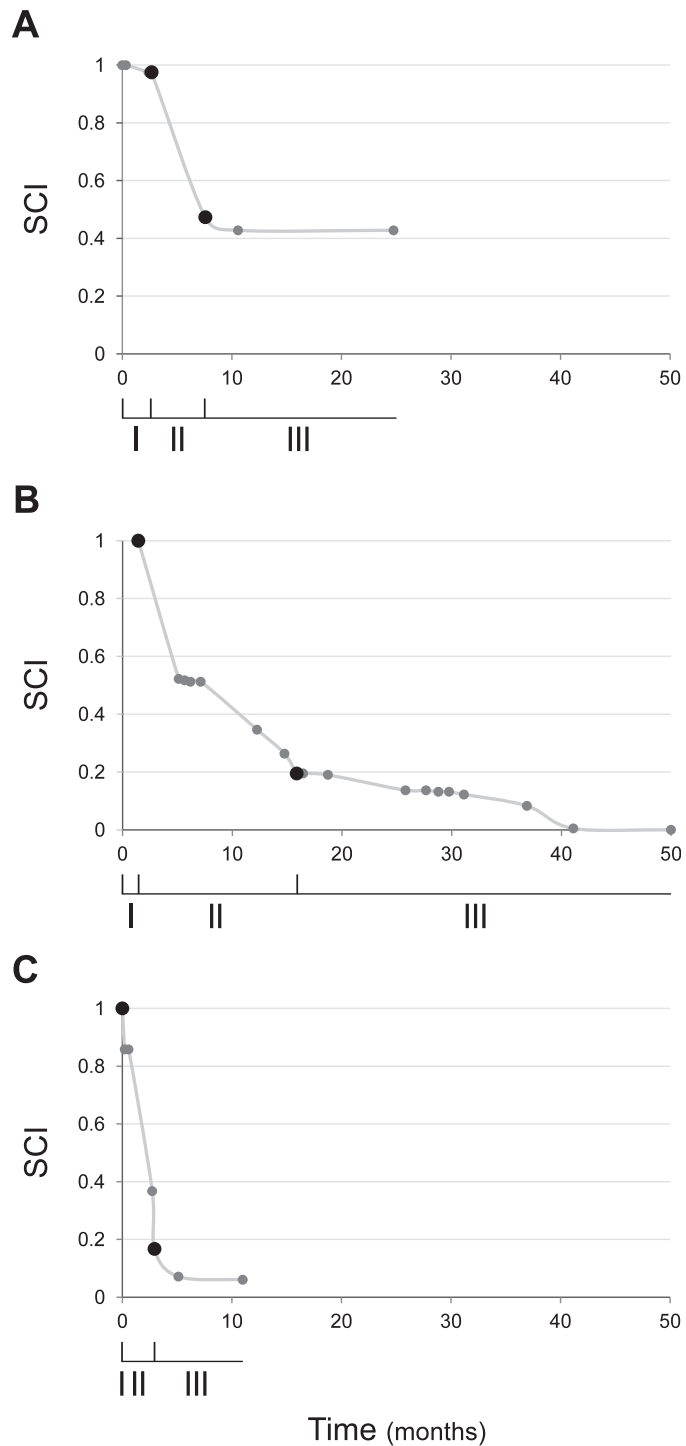


FIG. 2.—Example of degradation dynamics for three of the carcasses monitored in this study representing each of the three size classes: **A**) Class I (Vaca2). **B**) Class II (2Navas). **C**) Class III (Zorro). Key: dots = SCI values observed at different times during the monitoring; bold dots = observations defined as inflection points: the first one to occur is inflection point 1 (IP1) and the second is inflection point 2 (IP2). Phase I occurs from time 0 to IP1, Phase II from IP1 to IP2, and Phase III from IP2 to the end of the monitoring. The phases are also marked on the x-axis.

RESULTS

Data

Data were collected from the 32 carcasses for two to 63 months. Three carcasses were excluded from the analysis because they were not comparable to the rest of the carcasses: carcass 8UPA was naturally flooded by water during monitoring, and carcasses 9NAVAS and 12NAVAS were suspected to have been poisoned. These two carcasses remained complete for the two to four years of monitoring, at the end of which these carcasses were almost completely buried, one by vegetation and the other by normal aggradation of soil sediments. After excluding these three individuals, a total of 29 carcasses were used for analyzing the dynamics of carcass degradation (Table 1): four Class I carcasses from RBD, 23 Class II carcasses (13 from RBD and 10 from SNS) and two Class III carcasses from RBD. An example of the SCI dynamics for an individual of each size class is shown in Figure 2.

Factors Influencing Degradation Dynamics

Dynamics of SCI was significantly affected by time, size class, locality, and tree coverage. In a GLMM with these four variables included (see final model in Table S1), SCI significantly decreased over time, as expected (for variable $e^{-\text{time}}$, $\beta = 5.843$, $\text{SE} = 0.788$, $p < 10^{-12}$). Presence of tree coverage ($\beta = -0.664$, $\text{SE} = 0.266$, $p = 0.013$) and locality SNS ($\beta = -1.154$, $\text{SE} = 0.280$, $p < 10^{-4}$) had a negative effect on SCI (see figure in Online Supplemental File). Controlling for these variables, we found differences in SCI between the smaller size class (Class III) and the two larger classes (Class I and II). Class III showed significantly lower SCI values than the other two classes (compared to Class I: $\beta = -1.755$, $\text{SE} = 0.568$, $p = 0.002$; compared to Class II: $\beta = -2.176$, $\text{SE} = 0.515$, $p < 10^{-4}$) (Fig. 3). Initial condition of the carcass, species and age of the individual when death occurred had no significant effect over SCI values. Models and complete output are provided (see Online Supplemental File, Table S1).

Phases of Degradation

Data from 19 carcasses were sufficiently complete to estimate the velocity of bone loss between observations. We detected three different phases in the degradation process based on markedly different velocities of degradation. In Phase I the soft tissues were lost, but very few bones became disassociated from the rest of the skeleton. Bones were lost relatively quickly in Phase II when most of the soft tissue was gone, and then in Phase III entered a plateau where, once again, bones were lost at a very slow rate and they began to be incorporated into the sediment via normal aggradation of soil (Fig. 2).

The inflection point associated with the change from Phase I to Phase II was calculated in 19 cases, and the second inflection point associated with a change from Phase II to Phase III was calculated in 12 cases (see Table 1).

Phase I was characterized by the degradation of soft tissues and a very low rate of bone loss: 0.8 SCI/month on average (standard deviation, $\text{SD} = 1.1$, calculated over nine carcasses that had more than one observation in Phase I). Phase I lasted about a month (average = 27 days), consistent with the time observed (8–39 days) by Dabbs et al. (2013) for other Class II animals. At the end of this period, skeletons remained complete ($n = 14$) or nearly complete ($n = 5$), with an average SCI value of 0.99 ($\text{SD} = 0.01$, $n = 19$). No significant differences in SCI were found between classes at the end of this phase (Fig. 4a; Online Supplemental File, Table S2).

The first inflection point (inflection point 1) in the dynamics of degradation was detected by an increase in the velocity of bone loss (p) of 460–760% as compared to p in the previous period. At that moment, Phase II started. Velocity of bone loss was fastest in Phase II, at an average rate of 15.3 SCI/month ($\text{SD} = 9.0$, $n = 12$). Little soft tissue

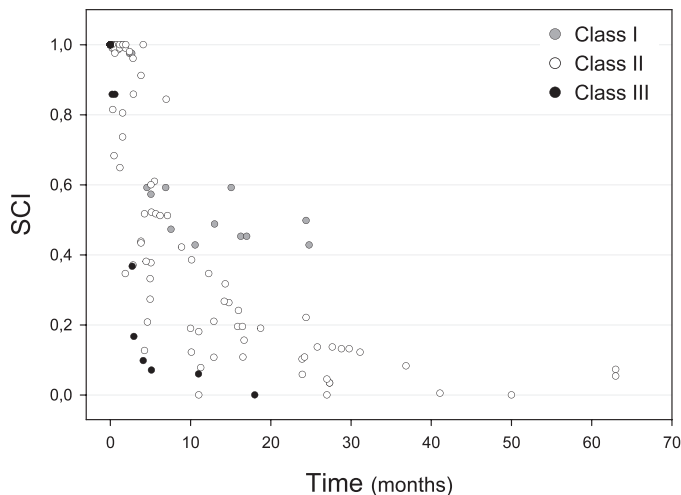


FIG. 3.—SCI values observed during carcass degradation for the 29 carcasses monitored and used in analyses in this study. Key: gray circles = observations from Class I carcasses; open circles = Class II carcasses; black circles = Class III carcasses.

was left on the carcasses in this phase. This phase lasted an average of 5.8 months.

Change from Phase II to Phase III occurred at inflection point 2, when the velocity of bone loss between two observations reduced to an average of 95% (range 85–100%) of the velocity observed in the previous period. At the point carcasses entered Phase III, Class I carcasses had an average SCI of 0.55 (SD = 0.06), Class II carcasses an average SCI of 0.26 (SD = 0.13), and Class III carcasses an average SCI of 0.13 (SD = 0.05), which was significantly lower than that for Class I ($\beta = -1.988$, SE = 0.414, $p < 10^{-5}$) and for Class II ($\beta = -1.414$, SE = 0.441, $p = 0.001$). These analyses were done controlling for locality, since SCI values were significantly lower in SNS than in RBD ($\beta = -1.004$, SE = 0.329, $p = 0.002$) (see Model 2 in Online Supplemental File, Table S3). We excluded data from SNS, which only had Class II carcasses, and analyzed only data from RBD, which had the three Classes represented. In this case, SCI at the inflection point 2 was significantly different between the three Classes (coefficients for Class I in the intercept, Class II $\beta = -0.590$, SE = 0.168, $p < 0.001$, Class III $\beta = -2.071$, SE = 0.216, $p < 10^{-16}$) (Fig. 4b; see Model 4 in Online Supplemental File, Table S3).

Phase III was characterized by a very low velocity of bone loss (1.1 SCI/month on average, SD = 1.2, $n = 12$) maintained for a long time until the disappearance of all bones, either through scavenging or through incorporation into the sediments. According to our observations, this phase could take from eight months to more than three years (both observations correspond to Class II carcasses). No carcasses of the largest class (Class I) were observed to completely disintegrate during the monitoring time (from 13 months to two years). Instead, their SCI maintained without changes around 0.50 (SD = 0.1, $n = 3$) across Phase III—for 16.3 months on average (SD = 3.5)—and after 22.1 months of degradation (on average, SD = 4.4). On the contrary, SCI values for carcasses of the two smaller size classes (Class II and III) were observed to reach lower values: 0.08 SCI on average for Class II (SD = 0.09, $n = 8$) after an average of 25.5 months of degradation (SD = 11.4); and 0.03 SCI on average for Class III (SD = 0.04, $n = 2$) after 14.5 months of degradation (on average, SD = 4.9). Models and complete output for each analysis are provided in the Online Supplemental File (Tables S2, S3).

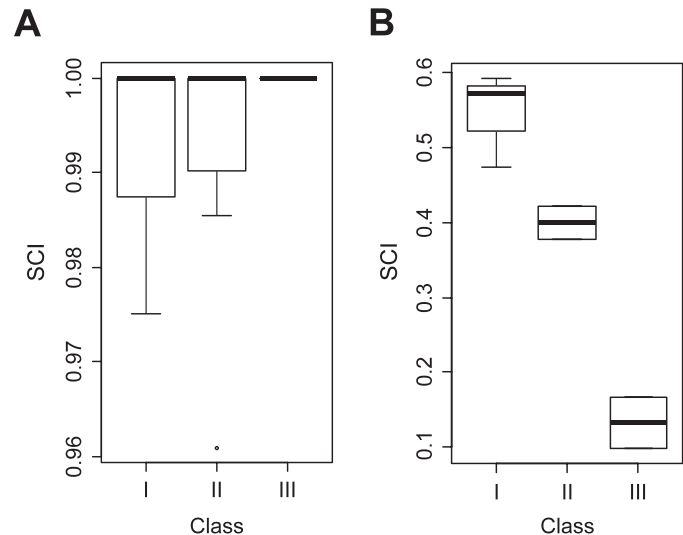


FIG. 4.—Boxplot of SCI by class in RBD. **A)** Inflection point 1 (IP1). **B)** Inflection point 2 (IP2). No differences in SCI were observed among classes at IP1, while significant differences were observed at IP2 for carcasses in RBD (see text).

DISCUSSION

Phases and Time Scales of Degradation

A general pattern of bone loss in three phases was observed for all size classes, consistent with Bernáldez Sánchez (2011). This pattern consisted of an initial phase (Phase I), in which only or primarily soft tissue was lost through scavenging and the velocity of bone loss was low. A number of papers have investigated carcass degradation in a forensic framework (e.g., Segura et al. 2011), and models and scoring systems for the degradation have been constructed with the goal of determining as precisely as possible the time since death of the animal (e.g., Moffatt et al. 2016). These studies primarily focus on Class II carcasses. On the scale of these studies, accumulated degree days (ADD), which takes into account temperature as well as time, has been found to be important as it impacts the development of insects and microorganisms. This body of work is relevant to the time a carcass spends in Phase I. Access to carcasses by scavengers also can have a dramatic effect on time spent in Phase I (Reeves 2009; Dabbs and Martin, 2013).

Once skeletonization is more or less complete, a phase of rapid bone loss (Phase II) follows, also primarily through scavenging. It is also possible that some bones are lost through other less common processes including bones being kicked far enough away that they were not findable, or transport by physical environmental processes. There is a series of papers, most notably by Andrew Hill and Anna Behrensmeyer, in which a serious attempt at quantifying disarticulation of large mammal skeletons was made, including a model which could be applied in a variety of situations (e.g., Hill 1978, 1979; Hill and Behrensmeyer 1984). In those articles, an argument was made that disarticulation is relevant to interpreting the paleoecological record because it is associated with dispersion (the spreading of bones, generally away from the carcass), and thus whether or not the bones eventually enter the fossil record. Whether disarticulation and bone loss (SCI) are directly relatable or not, they are different ways of measuring the degradation of the skeleton with an eye to the bones' eventual possible entrance into the fossil record. The data collected in these works was on the presence of intact articulations, the connection of bones by soft tissue. It is possible that this is related to bone loss, for example, if a joint is lost because it is removed from the site (either by a scavenger or other process). However, it is also possible for the joint to be lost without the bones being lost. Hill and Behrensmeyer found the

process of disarticulation to be a continuous process (Hill 1979; Hill and Behrensmeyer 1984), which is different from the pattern we found in bone loss. This difference could suggest that different factors are more important in these different proxies for fossil potential. The time frame of the studied disarticulation is primarily Phase II, although some of the skeletons were likely to be Phase III (the different skeletons of different ages were measured at a single point in time).

In the final phase, Phase III, bone loss slowed. In this phase the action of scavengers declines and degradation or incorporation into the fossil record becomes controlled primarily by physical, environmental factors. The six stages of bone weathering as defined by Behrensmeyer (1978) correspond primarily to Phase III bones.

Patterns of Degradation in the Different Size Classes

In some cases the smallest carcasses followed a different pattern in which both the soft tissue and the bones were rapidly consumed. This led to more variation in the degradation of the small carcasses, apparently due to whether or not they were found by a scavenger. If a carcass was found by a scavenger, it was likely to be completely or nearly completely consumed very rapidly. If it was not scavenged, it could stay complete for long periods of time. During one of our surveys, a stork carcass weighing around 5 kg was found. However, in the four hours it took to return to the find, the SCI had reduced from 100 to 0 (only four feathers were left). In another case a sub-adult rabbit carcass (~ 0.3 kg) was identified, and it too completely disappeared in a matter of a couple hours. These smaller carcasses may be subject to scavenging by a larger variety of animals, since animals such as fox and badgers may also be capable of consuming those smaller bones (Estévez and Mameli 2000; Pasda 2005). Much more data are needed in order to form a better picture of what happens to smaller carcasses, and at what size carcasses are able to be completely consumed by a range of animals, which increases variance in SCI in the period soon after death.

Different size classes had about the same SCI when they transitioned from Phase I to Phase II, but statistically different SCI as they entered Phase III (Fig. 4). This may reflect the ability of the scavenging community to process the bones. The smallest carcasses have the most fragile bones and thus are available to the largest number of scavengers. These carcasses degraded the fastest, and all or nearly all of the bones were lost in some cases. Young animals also have more fragile bones, but in these analyses age was not a significant factor. It is possible that this is due to insufficient sampling. The SCI value of some of the Class II carcasses also reached 0, but it was a smaller percentage of the cases. At the end of the study, after about two years, the SCI for all of the largest carcasses (Class I) were over 40. The difference in SCI for the different classes as they enter Phase III yields very different fossil potentiality for the different size classes. The largest animals had the largest SCI, suggesting that larger carcasses would tend to be over represented in the fossil record. This agrees with Behrensmeyer and Boaz's (1980) hypothesis that larger mammal carcasses have higher fossil potential than smaller ones.

Impact of Ecosystem

The carcasses degraded slightly differently in the two Mediterranean habitats studied here: SCI values were lower in SNS than in RBD. This could be due to the presence of the larger (Class I) carcasses in RBD, which maintain larger SCI values than the smaller classes. These two localities differ in characters such as overall frequency of tree cover and scavenger community. Both habitats have abundant populations of wild boar. SNS has a resident population of vultures, but they are only seasonal in RBD. Vulture presence may be one factor which accelerates Phase I (Reeves 2009), and differences in the vulture community may have important effects (Dabbs and Martin 2013). Vultures themselves are not

major consumers of bone, but they are able to open large carcasses and thus make those bones available to other scavengers, such as wild boar.

Tree coverage was included as a factor in the tests in order to better understand the role of vultures in these communities. Although SNS has, in general, more tree coverage than RBD, both ecosystems have both open and covered areas, and data were collected in both open and covered areas in both parks (Table 1). Therefore we were able to show that tree coverage had a significant impact on the SCI values observed. We observed higher rates of bone loss from carcasses in covered areas. Tree coverage could influence the scavenging pressure on carcasses since vultures detect carcasses mainly by spotting them while overflying open areas, while boars use their sense of smell to detect carcasses in open and covered areas. In some cases, it was observed that carcasses were moved from open areas to covered areas, apparently by boar, possibly to protect them from vultures. In areas with dense tree coverage, boars were able to access carcasses throughout the day. However, in more open areas vultures could exclude boar during their active period (the day).

Implications for the Fossil Record

These data suggest that in the course of interpretation of osseous remains from paleontological sites, it would be important to consider what scavengers capable of consuming bones of different size classes could have been present when the carcass was degrading, and the bones were in the process of being buried. For Mediterranean habitats during most of the Quaternary, this would include hyenas and hominids as well as boar. Avian scavengers such as vultures should also be considered. Although birds were unlikely to consume many bones, they could have moved bones away from the carcass or caused other scavengers to move bones or carcasses to protect (hide) them. When information about the paleohabitat is available, it would be relevant to consider that as well.

Accounting for the effect of the structure of the habitat and the locality (probably corresponding to scavenger community, in this case), size class had a significant effect on SCI values, but not species. Different individuals of the same species may be very different sizes, due, for example, to different developmental stages or sexual size dimorphism. So, in the interpretation of paleontological material, the size of the individuals seems to be more important than species identification for understanding taphonomy.

Another factor to consider while interpreting ancient remains is the observation that the bones associated with a single large carcass can become distributed over large areas by Phase II and III (Behrensmeyer and Boaz 1980; Bernáldez Sánchez 2009; Cáceres et al. 2009). In RBD we observed dispersal areas around 700 m². This means that a single large carcass may have bones over an area quite a bit larger than the average paleontological excavation. For example, the excavation of the Pleistocene site Venta Micena in southern Spain was 65 m² (Arribas and Palmqvist 1998), on the order of 10% of the area over which a single Class I carcass could reasonably be spread by the end of Phase II. So, more bones of single individuals of the larger animals may have been preserved in the fossil record than are identified because they are outside the study area, and so simply not identified in the excavation.

Finally, throughout the study we observed that bones of a single carcass were being buried by the normal aggradation of soil sediments unevenly. So, different bones of the same individual may degrade, weather, experience scavenging and enter the fossil record in an unequal manner.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <http://www.sepm.org/pages.aspx?pageid=332>.

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